Preliminary survival and abundance estimates for main Hawaiian Island insular false killer whales based on mark-recapture analyses of individual photo-identification data

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False killer whales (*Pseudorca crassidens*) are generally restricted to tropical and sub-tropical waters, although their density is highest in tropical waters (Ferguson and Barlow 2003). Even in the tropics they are relatively uncommon: Wade and Gerrodette (1993) noted they were the 11th most abundant of the 13 species of delphinids documented in the eastern tropical Pacific. Their life history is poorly documented, but they are known to mature at a relatively late age (e.g., females in one population were estimated to reach sexual maturity between 8.5 and 10 years of age), have long inter-birth intervals (estimated at seven years), and are relatively long-lived, with maximum longevity for males in the 50s and for females in the 60s (Ferreira et al. 2013). Their maximum rate of population growth has not been estimated. The rate of growth of one population of killer whales (*Orcinus orca*), a species with a similar life history, was 2.6% (95% CI of 2.48-2.76%) during a 23-year period of exponential population growth (Olesiuk et al. 2005).

Three stocks of false killer whales have been recognized within Hawaiian waters: the Hawai‘i pelagic stock, the main Hawaiian Islands insular stock, and the Northwestern Hawaiian Islands insular stock (Carretta et al. 2012). The main Hawaiian Islands insular stock has also been recognized as a Distinct Population Segment under the Endangered Species Act (Oleson et al. 2010), and was listed as Endangered in 2012. Abundance for this stock has been previously estimated using mark-recapture analyses of photo-identification data. The first estimate used photos from 2000 through 2004, and was undertaken prior to detailed information being available on the range of the population or movements of individuals among islands (Baird et al. 2005). A Bayesian multi-site closed population approach was used, with models that took into account sampling off different islands and interactions among the island areas. The model average abundance estimate from that approach, taking into account the proportion of distinctive individuals in the population, was 123 (CV = 0.72). More recently, open population models were applied to the same data set using the POPAN formulation (Schwarz and Arnason 1996) of the Jolly-Seber class of capture-recapture models. These abundance estimates were produced both for the 2000-2004 time period, and from the start of 2006 through September 2009. Preliminary abundance estimates were produced and presented to the Pacific Scientific Review Group in November 2009 (Baird 2009), although details of the outputs (e.g., apparent survival over the time periods) were not presented. At that time photographs were available from several groups of false killer whales encountered off of Kauaʻi that did not contain any known individuals from the main Hawaiian Islands population, and thus whose population identity was unclear. Estimates were produced both with and without these Kauaʻi individuals. However, since then those Kauaʻi individuals have been matched to individuals from the Northwestern Hawaiian Islands population (Baird et al. 2013a), and thus the estimate excluding those Kauaʻi individuals is the most appropriate. The highest ranking model (using AICc values) from the POPAN analysis using the 2000-2004 dataset resulted in an estimate of 162 individuals (CV = 0.23; Baird 2009), whereas the highest ranking model for the 2006-September 2009 dataset resulted in an estimate of 151 individuals (CV = 0.20; Baird 2009). These estimates were used in the status review (Oleson et al. 2010) and the 2006-September 2009 estimate of 151 individuals is currently used by NOAA Fisheries as the best estimate of abundance for this population (Carretta et al. 2012).

Since those earlier analyses, additional identification photographs have become available from more recent years (October 2009-2012), and additional work has been undertaken with the photo-identification catalog to reduce the likelihood of missed matches, that would have resulted in positively biased estimates of abundance. In addition, analyses of association patterns using photographic identifications available through 2010 have revealed the existence of a number of social units within the population, with three main social clusters identified (Baird et al. 2012). Movement data from satellite tagged individuals from two of these three social clusters (Clusters 1 and 3) indicate that individuals from both move regularly among the islands from Oʻahu to Hawaiʻi, although some differences in high density areas for the two clusters were identified (Baird et al. 2010, 2012). While no movement data from satellite tags are available from Cluster 2 individuals, re-sightings among islands suggest their movement patterns differ from either Cluster 1 or 3 individuals, with a disproportionate number of sightings of Cluster 2 individuals off Hawaiʻi Island (Baird et al. 2012). The three social clusters were not encountered at equal rates; Cluster 1 individuals were encountered greater than three times more frequently than either of the other two social clusters (Baird et al. 2012).

The purpose of this report is to present the results of analyses of abundance taking into account photographic identifications obtained from the main Hawaiian Island insular false killer whale population from 1998 through 2012, and also to present an estimate of non-calf survival for this population. These analyses are ongoing and these preliminary results should be interpreted with caution. In particular, analyses to be undertaken in the near future will incorporate effort as a covariate likely resulting in more robust estimates of abundance.

Methods

Photos of false killer whales were obtained through a variety of field efforts among the main Hawaiian Islands (see details of methods in Baird et al. 2008). Approximately 56% of all identifications were obtained through small-vessel surveys undertaken by Baird et al. (2013b), 40.5% were contributed by five major collaborating research groups (Table 1), and the remaining 2.9% of identifications were contributed by a number of other individuals and researchers. While effort data are available from most of the major contributors, we were not able to compile effort data from all sources prior to these analyses; thus we were not able to include effort as a covariate in the current analyses.

Photos in these analyses were considered from 1998 through 2012. Photos were sorted within each encounter by individual, and each individual was assigned a distinctiveness rating: 1) not distinctive; 2) slightly distinctive; 3) distinctive; 4) very distinctive. For each individual within each encounter the best quality photograph was also rated for photo quality as: 1) poor; 2) fair; 3) good; or 4) excellent. Analyses were restricted to good and excellent quality photos. Individuals of all distinctiveness ratings were considered when calculating the proportion of “marked” individuals within each encounter, with distinctive and very distinctive individuals being considered marked. Individuals were assigned to a social cluster following the methods outlined in Baird et al. (2012). Individuals not assigned to one of the three main social clusters were categorized into one of the three clusters based on proximity within the social network, as distance between individuals indicated relative association strength.

For determining the overall proportion of marked individuals in the population, the mean and standard deviation were calculated using all encounters with four or more identifications with good or excellent quality photos. Analyses were undertaken using the POPAN formulation of a Jolly-Seber model to estimate abundance and survival. These types of models are used to represent open populations and accommodate gains from births and immigration and losses from deaths and permanent emigration. In POPAN, the following parameters are estimated: apparent survival (Φ), capture probability (p), entry probability (*pent*), and abundance (N). Mortality and emigration are included in parameter Φ and are confounded. The abundance parameter is a super-population size and is defined as the total number of individuals that were in the population at some point during the period of the study. Parameter *pent(0)* corresponds to the proportion of the super-population available at the beginning of the study. The size of the population at the first occasion (year) corresponds to *pent(0)* multiplied by the super-population. The population size after the first occasion is computed as a function of the population in the year before, the apparent survival probability and the proportion of animals that enter the population. Estimates of model parameters and variances were carried out using the R (R Development Core Team 2012) package RMark v. 2.7.5[1] (Laake and Rexstad 2008). RMark is a collection of R functions used as an interface with program MARK for analysis of capture recapture data. We fitted and compared 32 POPAN models, which were constructed from all combinations of the following sub-models: 2 models for Φ (constant and variable by cluster), 4 models for p (constant, time, Time, and cluster), and 4 models for *pent* (constant, time, Time, and cluster). The ‘time’ model contains a parameter for each occasion in the dataset while the

[1]www.phidot.org/software/mark/rmark/

'Time' model contains an intercept and a slope and assumes a linear trend over time. Model weights were calculated using Akaike Information Criterion (AIC) (Burnham and Anderson 2002) and estimates of abundance and survival were averaged across all models, proportionally to their AIC weights. Chi-square tests 2 and 3 for the recapture-data were computed from RELEASE as a guide for goodness of fit test of a general model with full time-dependent effects. Year was chosen as our sampling period.

Results and Discussion

Between 1998 and 2012 there were 111 encounters with false killer whales with good or excellent quality identification photographs. Although we have not yet attempted to quantify effort for all possible data sources, to allow effort to be used as a covariate in abundance estimation, quantifying effort is problematic for several reasons. The number of encounters per year increased over time (Figure 1), reflecting an overall increase in effort, in part due to collaborators working off different islands beginning to contribute photos as the study progressed (Table 1). However, the average number identifications obtained per encounter varied among the collaborators, from an average of four identifications per encounter to an average of 12 identifications per encounter (Table 1), reflecting the amount of time different collaborators were able to spend with groups when encountered (since most of the collaborators were not focusing on false killer whale photo-identification), and the number of experienced photographers on board the vessels during encounters, among other things. Thus available measures of effort (e.g., number of days on the water per year) may not be strictly comparable among data sources. Even within a single group (e.g., Cascadia Research Collective), the number of good and excellent quality identification photos per encounter has increased over time (regression $p = 0.00878$, $r^2 = 0.1758$; Figure 2), likely reflecting both a continual improvement in the quality of cameras and lenses being used throughout the study, an increase in the number of photographers operating simultaneously (from one during early years to two or three in recent years), and learning about the wide-spread spatial nature of false killer whales groups part-way through the study (Baird et al. 2008), resulting in a greater number of sub-groups being photographed per encounter.

Over this 15 year period there were a total of 796 identifications (not excluding re-sightings) of distinctive or very distinctive individuals with good or excellent quality photographs; of these, 540 identifications were from Cluster 1, 91 identifications were from Cluster 2, and 165 identifications were from Cluster 3. More than half (475, 59.7%) were from Hawai'i Island, with 162 (20.3%) from Maui/Lana'i/Moloka'i, and 159 (20.0%) from O'ahu. The relative proportions of identifications from the different social clusters varied over the three shorter time periods for which we estimated abundance, with the proportion of identifications from Cluster 2 varying from 2.8% to 21.7% of all identifications (Table 2). The number of encounters per year generally increased over the 15 year period, as did the number of identifications of distinctive individuals (Figure 1), generally reflecting an increase in the number of collaborators providing photographs and overall effort. The estimate of the proportion of distinctive (marked) individuals in the population was 0.7521 (SD = 0.1516), based on 66 encounters with four or more individuals with good or excellent photo quality. This estimate is similar to the estimate used in the Baird (2009) analyses, based on a sample of 34 groups (0.747, SD = 0.143).

Using the 15-year dataset, of the 32 models run, there were two models that were given similar AIC weights (0.520 and 0.479, ∆AIC of 0.161 for the second model), accounting for almost 100% of the AIC weights. The top ranking model had cluster-dependent survival probability whereas the second model had fixed survival probability, and both models had time-dependent encounter probabilities, cluster-dependent probability of entries, and cluster-dependent super-population size. The estimates of average annual survival of marked animals (i.e., non-calves) ranged from 0.951 to 0.973 for the three different social clusters (Table 3). It should be noted that delphinid survival typically varies by age, with lowest survival rates at very young and very old ages, and relatively high survival rates in between (e.g., Olesiuk et al. 2005). Although some of the individuals in the photo-identification catalog were first documented in the 1980s (Baird et al. 2008), the ages of most individuals in the catalog are not known, thus it is not possible to assess how survival may change with age.

Estimates of abundance covering the same (2000-2004) or similar (2006-September 2009) time periods as the estimates presented by Baird (2009) were calculated, as was an estimate for the period from 2010-2012 (Table 4). Four models were run for comparison with Baird (2009), with survival (Φ) and capture probability (p) either constant or time-dependent. For the 2000-2004 period, the best model, responsible for 91.1% of the AIC weight, had constant survival and time-dependent capture probability. The model average estimate of the super-population size was 153 individuals (CV = 0.18). This estimate includes individuals born during the five year period as well as those that were alive at the start but died before the end of the five year period, thus there would be a positive bias when considering abundance for any particular year. For the 2006-2009 period it should be noted that the sample sets for the time period for this analysis was not identical to that used by Baird (2009); in our current analyses we added data from eight additional encounters between October and December 2009, and a number of missed matches were also identified after those analyses had been undertaken. For the 2006-2009 period the top model had time-dependent survival and capture probability, whereas the second choice model had constant survival and time-dependent capture probability. The two models had a ∆AIC of 1.1, and the resulting model-average estimate was 157 individuals (CV = 0.15). As with the previous estimate this includes individuals born during the four year period as well as those that were alive at the start but died before the end of the four year period, thus there would be a positive bias when considering abundance for any particular year. For the 2010-2012 period the top two models both had time-dependent survival, and fixed entry probability and abundance, with the top model having fixed capture probability and the second model (with a ∆AIC of 0.91) had time-dependent capture probability. The model-average estimate of abundance was 169 individuals (CV = 0.14). In all three cases the model-average parameter estimates produced unrealistically low estimates of survival (0.792 for 2000-2004; 0.812 for 2006-2009; 0.43 for 2010-2012). Resulting abundance estimates are thus likely subject to some degree of negative bias. Given the relatively low representation of Cluster 2 and Cluster 3 individuals in the 2006-2009 period, and Cluster 2 individuals in the 2000-2004 period (Table 2), these social clusters were likely not adequately sampled during these short-term periods.

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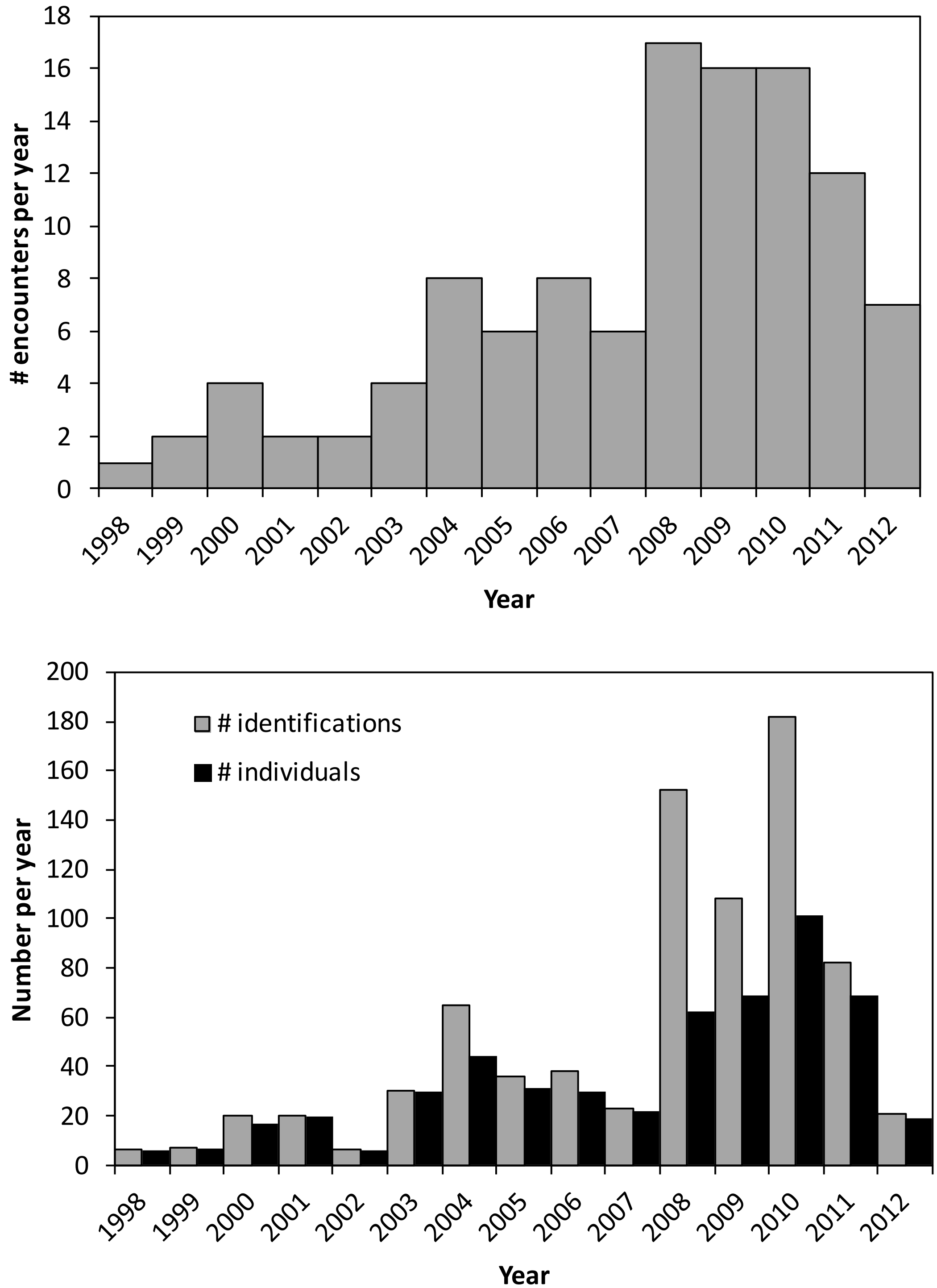

Figure 1. Top. Number of encounters with identification photos by year. Bottom. Number of identifications (including re-sightings within years) and number of distinctive individuals (excluding within-year re-sightings) by year, restricted to distinct and very distinct individuals with good and excellent quality photographs.

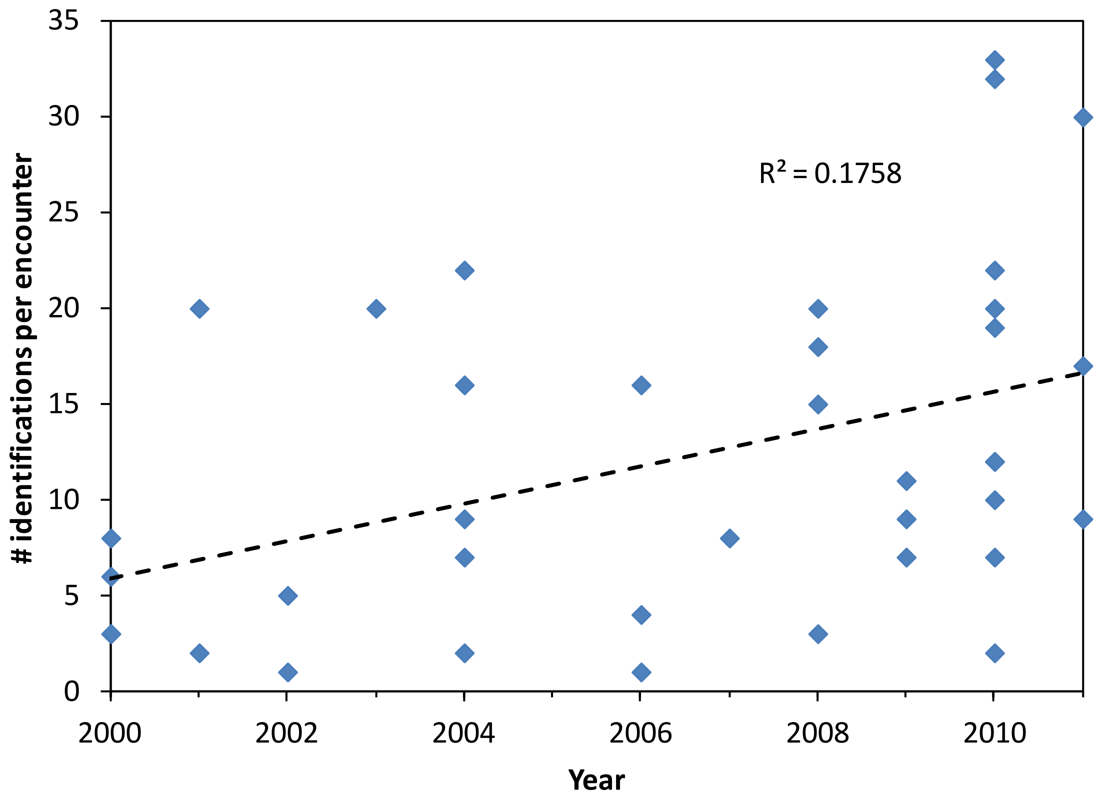

Figure 2. Number of identifications with good or excellent quality photographs by year restricted to Cascadia Research Collective encounters. The trend line and r^2 value for a regression ($p = 0.00878$) are shown.

Table 1. Contribution of false killer whale identifications to this study by source.

Source	% of total identifications	Mean # identifications per encounter	Islands photos available	Years photos available
Baird et al.	56.6	12	O‘ahu, Maui, Hawai‘i	00-04, 06-11
McSweeney	14.1	10	Hawai‘i	98-99, 05-06, 08, 11-12
Cullins	8.3	4	O‘ahu	06-12
Salden	7.2	6	Maui	03-06, 09-11
Deakos	5.7	8	Maui	03, 05, 11
PIFSC	5.2	4	O‘ahu, Hawai‘i	05, 09
All others	2.9	2	O‘ahu, Maui, Hawai‘i	99, 04, 06-12

Table 2. Distribution of identifications among false killer whale social clusters over three time periods.

Time period	Total identifications	Cluster 1 Number/%	Cluster 2 Number/%	Cluster 3 Number/%
2000-2004	141	61/43.2	11/7.8	69/48.9
2006-2009	321	260/80.9	9/2.8	52/16.2
2010-2012	285	179/62.8	62/21.7	44/15.4

Table 3. Model averaged estimates of false killer whale annual survival by social cluster, using data from 1998 through 2012.

Social Cluster	Estimate	SE	CV
1	0.973	0.01	0.01
2	0.965	0.015	0.016
3	0.951	0.023	0.024

Table 4. Model averaged estimates of abundance of false killer whales for two time periods. The first period corresponds to the analysis presented by Baird et al. (2005), and the second period generally corresponds to the period presented by Baird (2009) and used in Oleson et al. (2010), with the addition of photographs from October-December 2009.

Marked animals			
Period	N	SE	CV
2000-2004	115	17.5	0.15
2006-2009	119	5.6	0.05
2010-2012	127	4.2	0.03
Total population (corrected for unmarked animals)			
Period	N	SE	CV
2000-2004	153	27	0.18
2006-2009	157	23	0.15
2010-2012	169	25	0.14